

THE LOWER PERMIAN SYNAPSID *GLAUCOSAURUS* FROM TEXAS

by S. P. MODESTO

ABSTRACT. The early synapsid *Glaucosaurus megalops*, from the Lower Permian of north-central Texas, is re-examined. Despite being represented by a single, partial skull of uncertain ontogenetic age, the presence of six autapomorphies indicates that *Glaucosaurus* is clearly a distinct synapsid form. Phylogenetic analysis of the early Synapsida indicates that *Glaucosaurus* is the probable sister taxon of *Edaphosaurus* within Edaphosauridae. The clade of *Glaucosaurus* and *Edaphosaurus* is distinguished from its sister taxon *Ianthasaurus* by five synapomorphies: (1) premaxillary teeth equal to maxillary teeth in size, (2) caniniform region absent, (3) caniniform tooth absent, (4) prefrontal ventral process expanded transversely, and (5) transverse flange of pterygoid absent.

IN 1915 S. W. Williston erected the taxon *Glaucosaurus megalops* for a small partial skull recovered from the Mitchell Creek locality (Waggoner Ranch Formation, Wichita Group, Lower Permian) of Baylor County, Texas. He remarked that the skull of *Glaucosaurus* resembled that of the large edaphosaurid *Edaphosaurus*. However, the original preparation was poor and resulted in the elimination of many sutures. The partial preservation of the type and the unfortunate loss of discernible sutures has made *Glaucosaurus megalops* one of the most problematical of Permo-Carboniferous synapsid taxa.

Despite the fragmentary nature of the holotype, Broom (1932) re-examined it and allied *Glaucosaurus* with another early synapsid from Mitchell Creek, *Mycterosaurus longiceps*, and a South African form, *Anningia megalops*; the order Anningiamorpha was erected to encompass these three taxa (Broom 1932). *Mycterosaurus* has since been recognized as a varanopseid eupelycosaur (Berman and Reisz 1982), whereas *Anningia* and the order bearing its name were declared *nomina vana* (Reisz and Dilkes 1992).

In their monumental review of Permo-Carboniferous synapsids, Romer and Price (1940) noted that *Glaucosaurus* had little in common with any early synapsid other than *Edaphosaurus*, and identified *Glaucosaurus* as a primitive member of their (polyphyletic) synapsid suborder Edaphosauria, suggesting further a close relationship with *Casea*. This hypothesis was prompted by their assumption that both taxa had a single coronoid. However, *Casea* possesses two coronoids (Sigogneau-Russell and Russell 1974), and the fragmentary lower jaws of *Glaucosaurus* were only partially prepared; the sutural patterns of the mandible of *Glaucosaurus* could not have been determined faithfully in medial view.

More recently, Reisz (1986) concluded that *Glaucosaurus* possessed none of the apomorphies that defined the six major groups of Permo-Carboniferous synapsids, and regarded *Glaucosaurus* as a synapsid of uncertain phylogenetic affinities. He reiterated the remarks of Williston (1915), and Romer and Price (1940) that the general shape of the skull of *Glaucosaurus* resembled that of *Edaphosaurus*, but cautioned that the lack of discernible sutures would make its assignment to any of the established synapsid families quite tentative.

However, several studies in the past few years have greatly expanded our knowledge of the anatomy and interrelationships of eupelycosaurian synapsids (Reisz *et al.* 1992), including edaphosaurids (Reisz and Berman 1986; Modesto 1991; Modesto and Reisz 1992). Work on the oldest known edaphosaurid *Ianthasaurus* (Modesto and Reisz 1990) indicates that edaphosaurids

are united only by the distinctive morphology of their presacral neural spines. Hence, although *Glaucosaurus* is clearly not referable to most Permo-Carboniferous synapsid families, there is no cranial evidence excluding it from the Edaphosauridae. Since Modesto and Reisz (1992) asserted that the adaptation to terrestrial vertebrate herbivory arose within the edaphosaurid clade, the possibility that *Glaucosaurus* is a close relative of *Edaphosaurus* within Edaphosauridae is intriguing, and may provide evidence of the development of herbivory in the latter genus.

The holotype of *Glaucosaurus megalops* is therefore re-examined in order to determine if it is indeed a relative of *Edaphosaurus*, or if it represents a distinct eupelycosaurian form, with a phylogenetic position elsewhere on the synapsid tree.

MATERIALS

The holotype is the only specimen assigned to the taxon *Glaucosaurus megalops*. The teeth, antorbital margin, external nares, and inner aspect of the mandibles were prepared further with grinder and pin-vice. Preparation of the ventral aspect of the palate was hindered by the *in situ* preservation of the mandibles, and also by damage resulting from a drillhole, which had been bored into the skull from below (for mounting purposes).

For the phylogenetic review, specimens assigned to the synapsid taxa *Eothyris parkeyi* (MCZ 1161), *Edaphosaurus novomexicanus* (FMNH UC 674), and *Edaphosaurus boanerges* (MCZ 1762) were examined.

Institutional abbreviations are: FMNH UC, Field Museum of Natural History, University of Chicago; MCZ, Museum of Comparative Zoology, Harvard University.

SYSTEMATIC PALAEONTOLOGY

SYNAPSIDA Osborn, 1903

EUELYCOSAURIA Kemp, 1982

Family EDAPHOSAURIDAE Cope, 1882

Genus GLAUCOSAURUS Williston, 1915

Type species. *Glaucosaurus megalops* Williston, 1915.

Diagnosis. Short-snouted edaphosaurid eupelycosaur distinguished from all other synapsids by the presence of a prearticular that extends anteriorly as far as the jaw symphysis. *Glaucosaurus* is distinguished from other edaphosaurids by the following autapomorphies: septomaxilla exposed facially; three premaxillary teeth; maxilla long, extends posteriorly to posterior orbital margin; marginal teeth compressed laterally; subtemporal bar deeper dorso-ventrally than suborbital bar.

Glaucosaurus megalops Williston, 1915

Text-figures 1–3

1915 *Glaucosaurus megalops* Williston, p. 576, fig. 1.

1932 *Glaucosaurus megalops*; Broom, p. 15, fig. 2E–G.

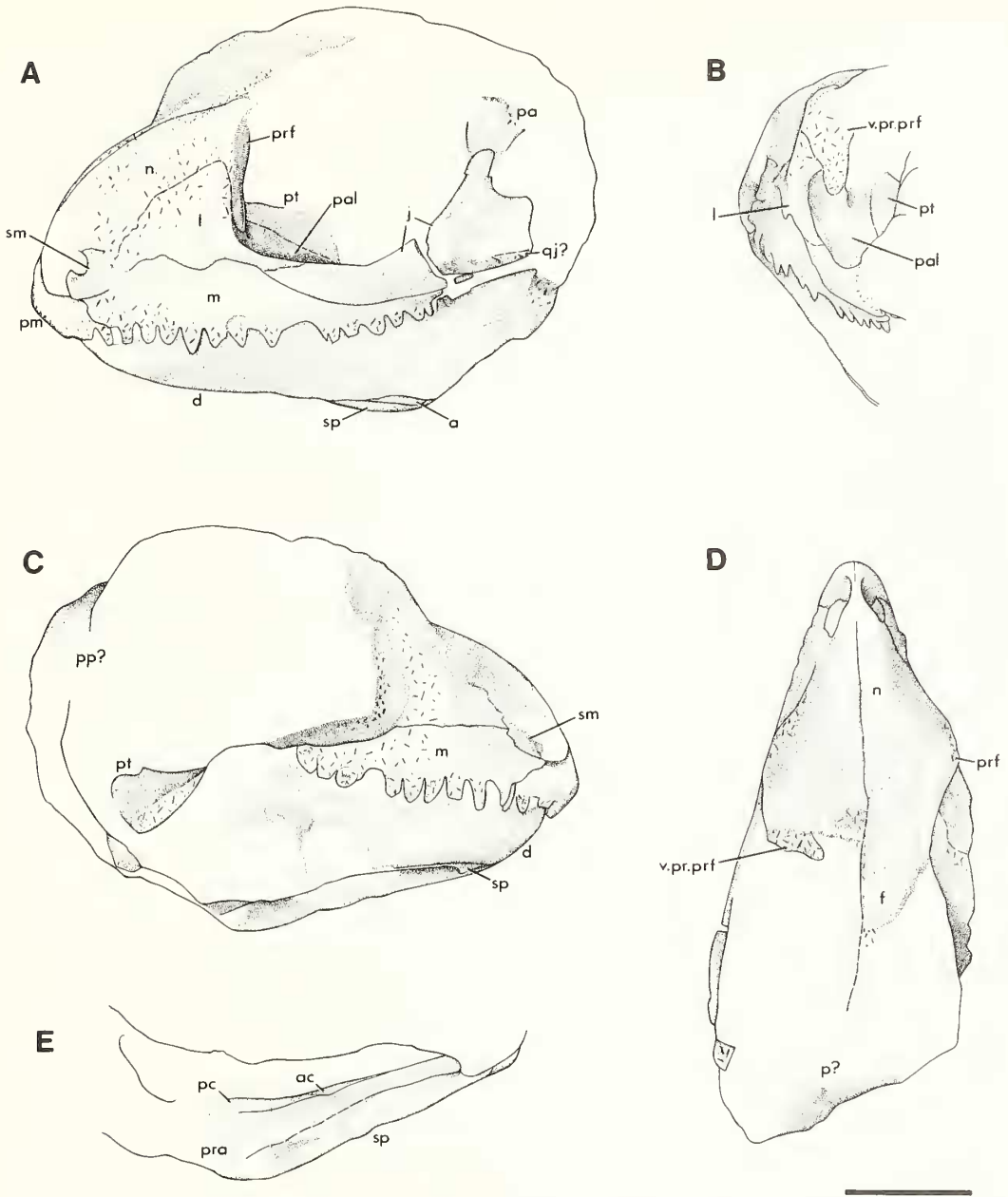
1940 *Glaucosaurus megalops*; Romer, and Price p. 507, pl. 20.

Diagnosis. As for genus, this being the only recognized species.

Locality and Horizon. Mitchell Creek, near Maybelle, Baylor County, Texas; Waggoner Ranch Formation (formerly Clyde Formation; see Hentz (1988) for stratigraphical review of north-central Texas), Wichita Group, Lower Permian.

Holotype. FMNH UC 691, the only known specimen.

Description. The skull (Text-fig. 1) is compressed obliquely and slightly transversely. Much of the skull roof, posterior cheek, occiput, and posterior ends of the mandibles are missing, and the braincase is absent. Most

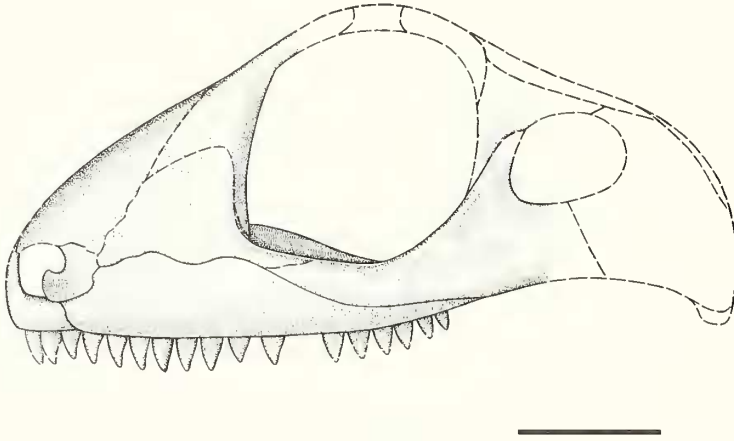


TEXT-FIG. 1. *Glaucosaurus megalops* Williston, 1915. FMNH UC 691, holotype. A, left lateral view of skull; B, posterolateral view of left antorbital region showing antorbital buttressing; C, right lateral view of skull; D, dorsal view of skull; E, ventromedial view of left mandible. Most of the sutures on the skull table were obliterated by previous preparators; for the purpose of clarity, their probable positions are not indicated. Scale bar represents 10 mm.

elements forming the dorsal margin of the orbits are preserved partly as impression, albeit poorly, but still give a fair indication of the size of the orbit. The surfaces of many elements, particularly the nasals, prefrontals, and lacrimals, are damaged by varying degrees of overpreparation. The palate is visible largely in dorsal view.

Although the relatively large orbits suggest immaturity, the ontogenetic age of the skull is uncertain as no endochondral elements are preserved.

The redescription permits a revised reconstruction of the skull in lateral view (Text-fig. 2). The unpreserved portions are restored using edaphosaurid sutural patterns. No reconstruction of the skull is offered in dorsal view, as many of the elements of the skull roof are either absent or damaged, and few of their sutures can be discerned faithfully.



TEXT-FIG. 2. *Glucosaurus megalops*. Restoration of skull roof in left lateral view. Scale bar represents 10 mm.

The premaxilla (Text-fig. 1A, C) resembles those of other eupelycosaurs, but the anterior ascending process is damaged and it is unclear how far posterodorsally it extended. Three teeth are present (*contra* Williston 1915). Judging from their basal diameters, these teeth were similar to the maxillary teeth in size.

The maxilla is a long, low element that extends posteriorly to the level of the postorbital bar (Text-fig. 1A). Despite crushing, its ventral margin appears to have been slightly convex in lateral aspect. There are fourteen teeth present in the complete left maxilla, with a position for one more, indicating that approximately eighteen teeth were present in each jaw. Although the labial surfaces have been planed away from most of the maxillary teeth, what remains of their profile, together with their subequal basal diameters, indicates that neither a caniniform tooth nor a caniniform region was present. The anteriormost teeth on the right maxilla are laterally compressed, slightly recurved, and sharply tipped. In contrast, the posteriormost tooth of the left maxilla is peg-shaped, and lacks the curvature and transverse flattening of the anterior teeth, which suggest that the posteriormost maxillary teeth were slightly more robust than the anterior teeth. There is no septomaxillary foramen in the expected position immediately posterior to the base of the septomaxilla. There is, however, an elongate perforation in the right maxilla immediately posterior to the septomaxilla, but it is unclear whether this opening represents either surface damage or a foramen the size of which has been exaggerated by overpreparation.

As in other early synapsids, the septomaxilla is a robust, vertical bone with a medial process that occupies the posterior half of the external naris (Text-fig. 1A). The septomaxilla is exposed facially, as its lateral surface is clearly confluent with that of the nasal, despite minor surface damage to the latter. Broom (1932) also interpreted a facial exposure for the septomaxilla, but restored it incorrectly as an elongate triangle of bone interposed between the lacrimal and the maxilla.

The triradiate jugal (Text-fig. 1A) resembles those of *Ianthasaurus* and *Haptodus* in general aspects, except that its subtemporal process is deeper dorso-ventrally than the suborbital process, and its ventral exposure is restricted between the maxilla and the quadratojugal. The jugal is slightly arched posteroventrally, indicating that the posterior cheek was emarginated as in edaphosaurids, sphenacodonts (*sensu* Reisz *et al.* 1992), and most ophiacodontids. The lateral surface is lightly sculpted with small, circular dimples. Along the ventral edge of the subtemporal bar of the jugal there appears to be a small fragment of bone, which previous investigators have identified as the anterior tip of the quadratojugal. If this is indeed the quadratojugal and not simply a product of crushing, then the quadratojugal would have formed the ventral edge of the subtemporal bar. A partial postorbital is preserved in association with the postorbital ramus of the jugal; it appears to be displaced slightly posteriorly.

Little can be said of the lacrimal except that it probably extended between the septomaxilla and the orbit, and forms the lateral portion of the antorbital buttress. Very little can be made of the surfaces and the margins of the nasals and the fragmentary frontals. The sculpturing on the skull table commented on by Lewis and Vaughn (1965) has been exaggerated by overpreparation.

The external surfaces of both prefrontals have been damaged by poor preservation and crushing, and their sutures with the nasals and lacrimal cannot be determined with certainty. The ventral process of the prefrontal, seen in posterior aspect and in frontal section (Text-fig. 1B, D), is greatly expanded transversely and appears to form most of the antorbital buttress. Overpreparation has removed the lacrimal-prefrontal suture, but the general shape of the ventral process of the prefrontal suggests that it contacted the palatine, as in *Edaphosaurus*.

An imperfectly preserved portion of bone is located posteriorly on the skull table where one would expect the parietal and the postparietal to lie (Text-fig. 1C–D). If identified correctly and not displaced too far anteroventrally by crushing, then this fragment suggests that the occiput sloped anterodorsally, as in other early synapsids.

The dorsal surface of the right half of the palate has been damaged by overpreparation and it is impossible to describe surface detail or sutural patterns except the probable suture with the maxilla. However, the dorsal surface of the left half of the palate is better preserved (Text-fig. 1B) and reveals that the palatine has a prominent dorsal process. Unfortunately, damage by previous preparators has obscured the sutures with the lacrimal and the prefrontal, and the suture between the palatine and the ectopterygoid is obscured by crushing. The dorsal process of the pterygoid (Text-fig. 1A) is dorso-ventrally low, as in *Edaphosaurus*. The palatal ramus of the pterygoid is arched slightly ventrally in parasagittal section, and there is no suggestion of a transverse flange. The palatal process does not appear to bear any teeth posteriorly, and only slight wear is present on its posterolateral edge (Text-fig. 1C).

Anteriorly, the dentary (Text-fig. 1C) is relatively deep as in caseosaurs and sphenacodonts, and not acuminate as reported by Williston (1915) and Romer and Price (1940). Only the last two dentary teeth are visible (Text-fig. 1A); they differ from the last maxillary tooth only by their smaller size.

The splenial (Text-fig. 1C, E) is exposed in lateral aspect only at the jaw symphysis and where it underlies the anterior tip of the angular. Medially, the splenial extends about halfway up the medial aspect of the mandible. The lingual surface of the left splenial has been subject to some crushing, and it is uncertain whether an inframeckelian foramen was present; the partial right splenial is uncrushed and shows no indication of such an opening anteriorly.

The prearticular is exceedingly long, extending posteriorly from the jaw symphysis (Text-fig. 1E). It increases slightly in dorsoventral height as one progresses posteriorly, at least as far as its preserved posterior end at the level of the last dentary tooth. Dorsal to the prearticular is a very slender splint of poorly preserved bone, which probably represents the anterior coronoid and the partial posterior coronoid. None of these elements possesses teeth.

PHYLOGENETIC RELATIONSHIPS

Re-examination of the holotype of *Glaucosaurus megalops* has uncovered several features that were overlooked by previous workers. *Glaucosaurus* possesses a suite of autapomorphies (see diagnosis) which indicates that this form cannot be recognized as a juvenile of any other synapsid taxon. *Glaucosaurus* also features two apomorphies (tall antorbital region, cheek concave posteriorly) that suggest a phylogenetic position within Eupelycosauria. In order to determine the most probable position of *Glaucosaurus megalops* within Synapsida, the interrelationships of the early synapsid families must be reexamined.

The following synapsid taxa, including *Glaucosaurus*, form the ingroup. Among caseosaurs, the caseid *Cotylorhynchus* (Romer and Price 1940; Stovall *et al.* 1966) is used, with additional information taken from *Casea* (Sigogneau-Russell and Russell 1974). *Eothyris* represents the family Eothyrididae; information on this form is taken from the holotype. The families Varanopseidae and Ophiacodontidae are represented by *Mycterosaurus* (Berman and Reisz 1982) and an undescribed ophiacodontid from the Upper Pennsylvanian of Kansas (Wilson 1989), respectively. Two edaphosaurid genera are used: *Ianthasaurus* (Modesto and Reisz 1990) and *Edaphosaurus* (Modesto 1991; Modesto and Reisz 1992). *Haptodus* (Laurin 1993) serves as a representative sphenacodont.

Two outgroups are used. The seymouriamorph *Seymouria* serves as the first outgroup (White 1939; Berman *et al.* 1987). The captorhinid reptile *Captorhinus* represents the second outgroup. The anatomy of *Captorhinus* (distinguished from '*Eocaptorhinus*' only by its multiple-tooth rowed

dentition) is well known from several recent papers (Holmes 1977; Heaton 1979; Dilkes and Reisz 1986).

Thirty-four characters were used in the analysis. The majority of these were taken from the literature (Brinkman and Eberth 1983; Reisz 1986; Gauthier *et al.* 1988), but a few are original. The analysis was run on a Macintosh IIsi computer using the branch-and-bound algorithm of PAUP 3.0, which is guaranteed to find the most parsimonious trees (Swofford 1989). All characters were optimized using DELTRAN, and run unordered.

Only one most parsimonious tree was found (Text-fig. 3). It requires sixty-one steps and has a consistency index of 0.60 excluding uninformative characters. The cladistic analysis supports the hypothesis of Reisz (1986) concerning the interrelationships of the six early synapsid families; characters diagnosing all nodes except node G have been discussed elsewhere (Reisz 1986; Modesto and Reisz 1992) and are not discussed here.

Interestingly, the tree indicates that *Glaucosaurus* is the sister taxon of *Edaphosaurus* within Edaphosauridae. This relationship is relatively robust, as three more steps would be necessary to remove *Glaucosaurus* from Edaphosauridae. This sister-group relationship is supported by the presence of five synapomorphies, which are described below. The number of the character is enclosed in parentheses; a character preceded by a minus sign indicates that it is a reversal, and ambiguous characters are denoted by an asterisk:

Premaxillary teeth equal to maxillary teeth in size (-2*). On the basis of basal cross-sectional diameter, the first premaxillary tooth is roughly equal to that of an average maxillary tooth in both *Glaucosaurus* and *Edaphosaurus*. However, because the premaxilla is known in *Ianthasaurus*, this character may apply at a more inclusive node. The presence of premaxillary teeth larger than maxillary teeth (except caniniforms) is primitive for synapsids.

Caniniform region absent (3). Neither *Glaucosaurus* nor *Edaphosaurus* features a caniniform region. The presence of a caniniform region, found in all other taxa examined here except caseids, represents the primitive condition.

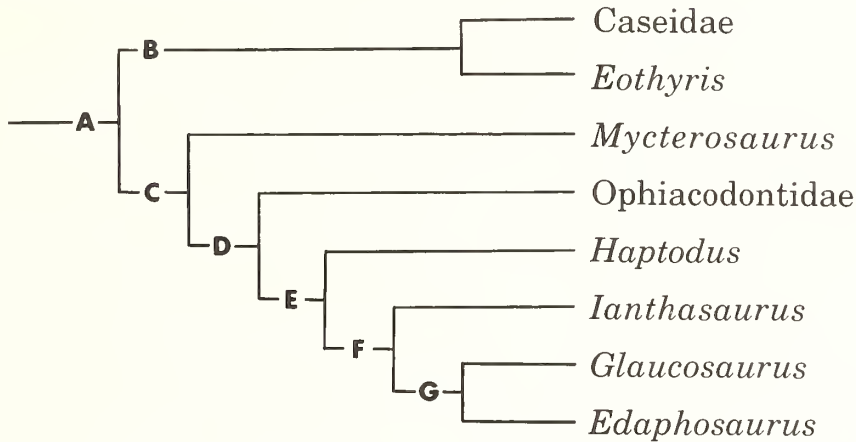
Caniniform tooth absent (4). There is no caniniform tooth in either *Glaucosaurus* or *Edaphosaurus*. The presence of a caniniform, defined here as a tooth whose basal diameter is notably greater than that of other maxillary teeth, represents the primitive condition.

Prefrontal ventral process expanded transversely (10). In *Glaucosaurus* and *Edaphosaurus* the ventral process of the prefrontal is greatly expanded transversely, and forms most of the antorbital buttress that is present in both taxa. The primitive condition of a prefrontal ventral process that is not expanded transversely is found in most other synapsids, including *Ianthasaurus*. *Eothyris* is interpreted here to have evolved the derived condition convergently.

Pterygoid transverse flange absent (22*). The pterygoid of *Glaucosaurus* and *Edaphosaurus* lacks a transverse flange. Because the palate is unknown for *Ianthasaurus*, this character may diagnose a more inclusive node. The presence of a transverse flange on the palatal ramus of the pterygoid is primitive for all other taxa examined here.

The absence of both the back of the skull and attributable postcrania has obscured past attempts to place *Glaucosaurus* among early synapsids. Although it has been suggested (Romer and Price 1940; Lewis and Vaughn 1965) that some of the postcrania from the Mitchell Creek locality, attributed originally to *Mycterosaurus* and clearly not edaphosaurid in nature, might belong to *Glaucosaurus*, this material was referred confidently to *Mycterosaurus* and to an unidentified temnospondyl amphibian by Berman and Reisz (1982). Traditionally, the absence of postcrania has excluded *Glaucosaurus* from the Edaphosauridae, as edaphosaurids are united only by their distinctive presacral neural spine morphology (Modesto and Reisz 1990). However, the fact that

edaphosaurids are united only by a few, albeit highly distinctive, postcranial characters is due partly to our inadequate knowledge of the oldest known member of the family, *Ianthasaurus hardestii*. The braincase, the palate, and most of the appendicular skeleton of this edaphosaurid are unknown (Reisz and Berman 1986; Modesto and Reisz 1990). Hence, the description of new *Ianthasaurus* material (and, similarly, the discovery of *Glaucosaurus* postcranial material) should provide new information that would either strengthen or require an emendation of the interrelationships of the three edaphosaurid genera given here.



TEXT-FIG. 3. Cladogram illustrating a hypothesis of relationships for *Glaucosaurus megalops*. Outgroup taxa used in the analysis are not shown. Nodes are defined by the following unambiguous characters: A (defining Synapsida), septomaxilla vertically oriented with medial process, lateral temporal opening present, occiput slopes anterodorsally. B (defining Caseosauria), frontal contribution to orbital margin reduced. C (defining Eupelycosauria), antorbital region tall, supratemporal narrow, parietal foramen positioned posteriorly on interparietal suture. D, jugal separates maxilla and quadratojugal, posterior cheek margin concave, stapes articulates in pocket on opisthotic, angular with ventral keel. E, quadratojugal reduced in size, prearticular twisted. F (defining Edaphosauridae), presacral neural spines with lateral tubercles, presacral neural spines subcircular in cross section, anterior presacral neural spines lean anteriorly, posterior presacral neural spines curve posteriorly. G, caniniform region absent, caniniform tooth absent, prefrontal ventral process expanded medially.

The addition of *Glaucosaurus* to the Edaphosauridae provides valuable insight into the evolution of herbivory in edaphosaurids. As the sister taxon of *Edaphosaurus*, *Glaucosaurus* features several characters which have been attributed to the adaptation to herbivory in *Edaphosaurus* (Modesto 1991). These include the presence of an antorbital buttress, isodonty, loss of the transverse flange of the pterygoid, and perhaps also the presence of an abbreviated snout. Ancestrally, edaphosaurids may have fed upon soft-bodied arthropods, a diet that has been proposed for *Ianthasaurus* (Reisz and Berman 1986). The ancestor of *Glaucosaurus* and *Edaphosaurus* may have progressed to a (possibly omnivorous) diet of harder foods; this is suggested by the short, buttressed antorbital region and isodonty present in both daughter taxa. *Glaucosaurus* may have been specialized for feeding upon hard-bodied arthropods, judging from the presence of sharp, laterally-compressed teeth, whereas *Edaphosaurus* evolved true herbivory.

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ABBREVIATIONS USED IN THE TEXT-FIGURES

a	angular	n	nasal	pra	prearticular
ac	anterior coronoid	p	parietal	prf	prefrontal
d	dentary	pal	palatine	pt	pterygoid
f	frontal	pc	posterior coronoid	qj	quadratojugal
j	jugal	po	postorbital	sm	septomaxilla
l	lacrimial	pm	premaxilla	sp	splenal
m	maxilla	pp	postparietal	v.pr.prf	ventral process of prefrontal

APPENDIX 1

Description of the characters used in the phylogenetic analysis. Characters are listed in order of their location on the skull, the mandible, and the postcranial skeleton.

1. Marginal teeth: taper gradually (0) or are slightly bulbous (1).
2. Premaxillary dentition: first tooth equal to or smaller than (0) or larger than maxillary teeth (1) in basal cross-section.
3. Caniniform region: present (0) or absent (1).
4. Caniniform tooth: absent (0) or present (1).
5. Maxillary teeth: subconical (0) or compressed laterally (1).
6. Maxilla: contacts (0) or separated from (1) quadratojugal.
7. Maxilla: short, does not extend posterior to posterior orbital margin (0) or long, extending past orbit (1).
8. Septomaxilla: sheet-like and curved (0) or oriented vertically with medial flange (1).
9. Antorbital region: low (0) or tall (1).
10. Prefrontal ventral process: laterally compressed (0) or expanded transversely (1).
11. Frontal: bounded by pre- and postfrontal laterally (0), separates pre- and postfrontals (1) and with broad orbital exposure (2).
12. Supraorbital margin: weakly developed (0) or expanded laterally (1).
13. Parietal foramen: positioned anteriorly (0), at midpoint of (1), or posteriorly (2) on interparietal suture.
14. Supratemporal: large, broad (0) or long, narrow (1).
15. Quadratojugal: large and contributes to subtemporal bar (0) or small and covered laterally by squamosal (1).
16. Lateral temporal fenestra: absent (0) or present (1).
17. Posterior cheek margin: straight (0) or concave (1).
18. Skull: long, eight dorsal centra or more in length (0), or short, six dorsal centra or less in length (1).
19. Postorbital region: shorter than (0) or equal to or longer than (1) antorbital region.
20. Occiput: vertical (0) or slopes anterodorsally (1).
21. Stapes: dorsal process free (0) or articulates in pocket on opisthotic (1).
22. Pterygoid: transverse flange present (0) or absent (1).
23. Prearticular: straight (0) or twisted posteriorly (1).
24. Angular: ventral keel absent (0) or present (1).
25. Cervical centra: equal to or longer than (0) or shorter than (1) mid-dorsal centra.
26. Presacral neural spines: laterally compressed (0) or subcircular (1) in distal cross section.

27. Presacral neural spines: anterior spines extend dorsally (0) or lean anteriorly (1).
 28. Presacral neural spines: posterior spines extend dorsally (0) or curve posteriorly (1).
 29. Presacral neural spines: lateral tubercles absent (0) or present (1).
 30. Neural arches: not excavated (0) or excavated (1).
 31. Dorsal vertebrae: transverse processes moderately developed (0) or elongate (1).
 32. Dorsal ribs: curved proximally (0) or curved throughout length (1).
 33. Dorsal ribs: tubercula well developed (0) or greatly reduced (1).
 34. Ilium: anterodorsal process absent (0), moderately developed (1), or strongly developed (2).

APPENDIX 2

Distribution of the character states among the taxa examined in the analysis. The numbers in the top column (1–34) refer to the characters described in Appendix 1. A question mark indicates that the character state could not be determined because of missing data.

Character number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Taxon																	
<i>Seymouria</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Captorhinus</i>	0	1	0	1	0	1	0	0	0	1	2	0	0	0	0	0	0
Caseidae	1	1	1	0	0	0	0	1	1	0	0	1	0	0	0	0	1
<i>Eothyris</i>	0	0	0	1	0	0	1	?	0	1	1	0	1	0	0	1	0
<i>Mycterosaurus</i>	0	1	0	1	1	0	1	?	1	0	2	0	2	1	0	1	0
Ophiacodontidae	0	1	0	1	0	1	0	?	1	0	2	0	2	1	0	1	1
<i>Haptodus</i>	0	1	0	1	1	1	0	1	1	0	2	0	2	1	1	1	1
<i>Glaucosaurus</i>	0	0	1	0	1	1	1	1	1	1	?	0	?	?	?	1	1
<i>Ianthasaurus</i>	0	?	0	1	0	1	0	?	1	0	2	0	1	1	1	1	1
<i>Edaphosaurus</i>	1	0	1	0	0	1	0	1	1	1	1	1	1	1	1	1	1
Character number	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
Taxon																	
<i>Seymouria</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Captorhinus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Caseidae	1	0	1	0	0	0	0	1	0	0	0	0	0	1	1	2	2
<i>Eothyris</i>	?	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mycterosaurus</i>	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ophiacodontidae	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Haptodus</i>	0	1	1	1	0	1	1	0	0	0	0	0	1	0	0	0	0
<i>Glaucosaurus</i>	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ianthasaurus</i>	0	1	1	?	?	1	1	0	1	1	1	1	1	0	0	0	1
<i>Edaphosaurus</i>	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	2	2